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GENETICAL STUDIES ON ŒNOTHERA. I

Notes on the Behavior of Certain Hybrids of Œnothera in the First Generation

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The following account is a report on the behavior in the first generation of the following sets of hybrids of *Œnothera* grown in the Harvard botanic garden in the summer of 1909: (1) *gigas* × *Lamarckiana*, (2) *muricata* × *gigas*, (3) *muricata* × *grandiflora*, (4) *biennis* × *grandiflora*, (5) *grandiflora* × *biennis*. The hybrids were not grown on an extensive scale, but represented rather a selection from the seedlings of the best plants in order to obtain for a special purpose the most vigorous crosses possible. The cross pollination was made in the writer's garden at Woods Hole in 1908, and the hybrids started in the hothouses at Cambridge early in January, 1909. Large rosettes were in most cases developed by the last of May, when the selected plants were set out in the botanic garden. All of the hybrids matured during the summer except a few plants of the cross *gigas* × *Lamarckiana*, which persisted in the rosette condition.

1. *gigas* × *Lamarckiana*. The parent forms of this cross were grown from seeds of De Vries, *Lamarckiana* having 14 chromosomes and *gigas* showing from a preliminary examination apparently twice this number. Twelve rosettes were planted exhibiting wide variation in the forms of the leaves, eight being similar to *Lamarckiana* and four similar to *gigas*. Two of the *Lamarckiana*-like rosettes and three of the *gigas*-like remained as rosettes throughout the summer, the former at the end of the summer being 3.5–3.7 dm. broad with leaves narrower than those of *gigas*, lanceolate and narrowly spatulate in form, the *gigas*-like being 4.5–5 dm. broad and indistinguishable from those of *gigas*.

Seven of the rosettes developed into mature plants which were similar to one another, 1–1.1 m. high with the characteristic habit and foliage of *gigas;* the large flowers and stout buds, ovaries and seed capsules, were also *gigas*-like. Some eighty attempts to obtain seed by guarded self pollination gave complete failures, which were the more interesting because ovaries presumably pollinated from neighboring *Œnotheras* by the numerous insect visitors matured large fruits and quantities of seeds; the failure to self-pollinate was thus apparently not due to abnormalities of the ovules. De Vries[1] reports that he has obtained fertile seed of this hybrid as well as of the reciprocal cross. There was a large proportion of abortive pollen, perhaps 80–90 per cent., but the remaining grains, as regards outward appearances, seemed normal. These latter consisted of a mixture of 3-lobed and 4-lobed grains in various proportions for different plants, the 3-lobed preponderating. Four-lobed pollen grains, as reported by Miss Lutz,[2] are characteristic of *gigas.*

2. *muricata* × *gigas.* The *gigas* parent furnishing the pollen of this cross was the same as in the preceding culture; the *muricata* parent was a wild plant from Woods Hole transplanted as a rosette to the garden of 1908. Hybrids of these were among the most interesting of the cultures of 1909. The well-developed rosettes were strikingly intermediate between those of the two parents, but fell clearly into two groups. Of the twelve plants in the culture six rosettes had leaves *muricata*-like in form but of a larger size than is typical of this species, and six rosettes had leaves broader than the above and conspicuously crinkled like the *gigas* parent.

The mature plants exhibited a similar difference; the first six had a habit and foliage that were *muricata*-like, the leaves, however, being longer and 2–3 times as broad; the other six plants presented a much stockier *gigas*-like habit with a stouter main stem and with leaves, which on the lower portion of the stem were strongly crinkled as in *gigas.* The flowers, inflorescences and capsules were quite similar in both groups of hybrids and presented forms and measurements intermediate between the two parents. The flowers, however, were decidedly smaller than the mean, and resembled those of the female *muricata* parent although about twice as large. The hybrids then as regards habit and foliage fell in about equal proportions into two groups, with greater resemblances to one or the other of the two parents. They presented an admirable illustration of the type of crosses called by De Vries[3] "twin hybrids", and reported for crosses between the *Onagra* group and *Lamarckiana,* or one of its derivatives, when these latter furnish the pollen.

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[1] De Vries, H. ('08*b*), "Bastarde von Œnothera gigas," *Ber. deut. bot. Gesell.*, XXVIa, 754, 1908.

[2] Lutz, Anne M., "Notes on the First Generation Hybrid of *Œnothera lata* × *O. gigas.*" *Science*, XXIX, 263, 1909.

These hybrids when self-pollinated set an abundance of seed which germinated readily, in sharp contrast to the experience recorded above for the hybrids of *gigas* × *Lamarckiana.* De Vries ('08*b,* p. 761) reports that hybrids of this cross as well as of the reciprocal have proved entirely sterile in his cultures. The fertility of my cross is especially interesting since we are dealing with a hybrid one of whose parents (*gigas*) has twice as many chromosomes as the other. A large proportion of the pollen grains, 75 per cent. or more, was abortive; the normal grains were almost wholly of the 3-lobed form (as in *muricata*), 4-lobed examples being uncommon.

3. *muricata* × *grandiflora.* There were two cultures of these hybrids based on two *muricata* parents from Woods Hole, pollinated, however, from the same *grandiflora* plant which was used in the crosses of *biennis* and *grandiflora,* a plant which is described somewhat fully below. The cultures comprised twenty-nine plants which did not pass through conspicuous rosette stages in the hot houses, but quickly developed the main stems, which were 1–2 dm. high when the plants were set out in the garden. Somewhat later these young plants with main stems 4–6 dm. high presented clearly a foliage intermediate between the parent types in form, color and texture. Thus the leaves were narrower, thicker, and a

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[3] De Vries, H. ('07), "On Twin Hybrids," *Bot. Gaz.*, XLIV., 401, 1907. ('08*a*), "Ueber die Zwillingsbastarde von *Œnothera nanella*," *Ber. deut. bot. Gesell.*, XXVIa, 667, 1908.

darker green than those of *grandiflora,* but broader, thinner, and a lighter green than those of *muricata.*

On reaching maturity four plants exhibited flowers almost as large as those of *grandiflora,* and a habit and foliage more like this parent than was shown by the other hybrids; these four plants were, however, only 1.2 m. high while neighboring *grandifloras* were 1.5 m. high and much more extensively branched. The remaining hybrids, twenty-five in number, were strikingly *muricata*-like in habit and foliage except that the leaves were broader than those of that parent and the flowers more than twice as large, in size somewhat midway between the small flowers of *muricata* and the very large flowers of *grandiflora.* These hybrids then, as in the case of the *muricata* × *gigas,* fell into two groups (twin hybrids) with marked resemblances to one or the other of the parents, but with all structural characters blended. The proportion of four *grandiflora*-like to twenty-five *muricata*-like forms probably does not represent the normal ratio between the plants of these two groups which would be expected to appear in about equal numbers.

There was certainly no evidence from the cultures of any tendency on the part of the hybrids to resemble markedly the male parents (patroclinous) as was reported by De Vries ('07) to be the rule among *Œnothera* hybrids of the *Onagra* group. On the contrary five sixths of the hybrids were strikingly similar to the female parent, although, as stated above, it is not likely that these proportions represent normal ratios.

4. *biennis* × *grandiflora.* The parents of this cross were carefully selected with an end in view. The *biennis* plant was found wild at Woods Hole and transferred to the garden of 1908; it was chosen as representative of the broader-leaved types of this variable species with, however, only medium-sized flowers. This strain of *biennis* has proved constant in the cultures of 1909, presenting the characteristic *biennis* habit of a main stem about 1 m. high and long side branches arising from near the base of the plant. The *grandiflora* parent was one of nine plants grown from seed collected by S. M. Tracy

at Dixie Landing near Tensaw, Alabama, a well-known locality for the species. It was selected because of the breadth of the leaves, which in this species present a wide range of variation from lanceolate to broadly elliptical, and for the reddish coloration of the sepals which in other forms of *grandiflora* may be a clear green. This plant in the Woods Hole garden grew to be 2.1 m. high and presented a habit characterized by a strong main stem and long side branches rising from near its base.

Eight plants of this cross were brought to maturity in the garden of 1909 and exhibited a wide range of form. Seven of them were markedly *grandiflora*-like in habit and foliage, but with shorter main stems, 1.1–1.5 m. high; the flowers were somewhat smaller than those of the *grandiflora* parent. It is not safe, however, in a relatively small culture to draw conclusions from this large proportion of the hybrids resembling the male parent (patroclinous), especially since in the reciprocal cross described below approximately half of the plants resembled the female parent.

One of the hybrids (*9ba*) proved interesting for its resemblance in certain respects to *Œnothera Lamarckiana*. This plant was 1.3 m. high with a strong main stem and the side branches, as in *Lamarckiana,* well distributed along the axis, in contrast to the origin of the chief side branches from near the base of the plant which is generally characteristic of both *biennis* and *grandiflora.* The flowers were intermediate in their measurements between the *biennis* and *grandiflora* parents and so similar to those of *Lamarckiana* as to be practically indistinguishable in the features that would enter into a taxonomic description of the flowers of the latter. The differences (such as a slightly greater length of the stigma lobes) were probably no greater than would be found among the flowers of any culture of *Lamarckiana* which included a fair representation of the range of variation presented by this form.

The important differences between this hybrid plant and *Lamarckiana* were concerned then with the foliage, but were very marked. The leaves in general were *biennis*-like in form, but slightly larger in their measurements. Those on the lower portion of the main stem, which in *Lamarckiana* are 20 cm. or more in length and much crinkled, were in the hybrid only 11 cm. long and exhibited only a very slightly crinkled surface. The leaves along the upper portions of the branches and the bracts of the inflorescences were on the contrary larger than those of *Lamarckiana* and the inflorescence was, therefore, conspicuously larger leaved. The rosette condition of this plant, as grown in the hot house, was too transitory to give satisfactory conclusions as to what its characteristics would have been if given the opportunity of a more prolonged development.

This hybrid set seed abundantly when the flowers were self-pollinated. Less than 50 per cent. of the pollen was abortive. The normal grains were almost entirely 3-lobed like the pollen of the parents, but occasional 4-lobed grains were present.

5. *grandiflora* × *biennis*. The parents of this reciprocal cross were the same individual plants employed in the preceding (4). The culture consisted of twenty plants which fell clearly into two groups (twin hybrids) with greater resemblances to one or the other of the parent forms.

Nine of the hybrids were *grandiflora*-like in foliage and habit, the leaves being lanceolate in form, longer, narrower and more pointed than those of *biennis*, and the plants taller (1.3 m.), presenting also the numerous heavily flowered side shoots characteristic of *grandiflora*. The flowers were intermediate in form and measurements between those of the parent types, and essentially similar to the flowers of *Lamarckiana*. Five of these hybrids developed large rosettes with leaves similar in form to those of *biennis* but more pointed; the leaves of four of the rosettes exhibited marked crinkles like those of *Lamarckiana*.

The remainder of the hybrids of this cross resembled the *biennis* parent in foliage and habit. The leaves were broadly elliptical or ovate in form, shorter than those of the *grandiflora*-like hybrids, and thicker in texture. The plants were shorter (.8–1.1 m. high) and the habit *biennis*-like in being sparingly branched, the side branches arising from near the base of the plant and being almost as long as the main stem. The flowers were intermediate between the parent types, but exhibited a somewhat greater range of measurements than those of the *grandiflora*-like crosses.

In three of these *biennis*-like hybrids (*9ba*, *9bb* and *9bc*) the flowers and inflorescences presented a structure so similar to that of *Lamarckiana* that they matched in all essentials the branches on certain *Lamarckiana* plants in the garden. The differences in the form of the bracts and parts of the flower were of the sort that can be observed in any reasonably large culture of *Lamarckiana*.

There were, however, striking differences between these three hybrid plants and *Lamarckiana* with respect to their foliage and habit of growth. The leaves on the lower portion of the stem were only 9–11 cm. long, about half the length of leaves similarly placed on *Lamarckiana*, and there were only slight traces of the crinkles so characteristic of *Lamarckiana*. The *biennis*-like habit of putting out long side branches from near the base of the plant was also very different from the usual habit of *Lamarckiana* in which the prominent side branches are more regularly distributed along the main stem.

These plants formed such transient rosettes in the hothouse that no conclusions could be drawn as to what would be their characters if allowed to develop more slowly. Seed was produced in abundance by self-pollinated flowers. Less than 50 per cent. of the pollen was abortive, the normal pollen, except for an occasional 4-lobed grain, was entirely 3-lobed.

GENERAL CONSIDERATIONS

While it is impossible to draw broad conclusions from these hybrids, which have as yet been observed only in the F_1 generation, a number of interesting points may be noted:

1. The characters of the parents, as presented in each

cross, were so blended that as regards the measurements of parts, habit, texture of foliage, etc., the average for each set of hybrids would probably present a fair mean between the two parents concerned. There was, however, a wide variation in the resemblance of the hybrids to one or the other of the parents.

2. No character of either parent was discovered which appeared as dominant in these hybrids of the F_1 generation, after the manner which has been described for certain forms (*e. g., Pisum*) that illustrate most conspicuously Mendelian dominance in the first generation.

3. Some of the hybrids of each cross presented a greater resemblance to one parent and some to the other, and the forms could therefore be arranged in two groups (twin hybrids) in one of which the maternal characters were most evident and in the other the paternal. There was no clear evidence that the hybrids of these cultures carried in marked preponderance the paternal characters (patroclinous), or on the other hand that maternal characters were more prominent. The range of variation among the hybrids was too great to permit of such conclusions.

It becomes a matter of interest to determine how plastic these hybrids will prove to be in later generations, and whether or not they will exhibit variations that may be fixed and accentuated by artificial selection. This line of enquiry will be especially pertinent to the behavior of those hybrid plants of *biennis* and *grandiflora* which in this F_1 generation presented *Lamarckiana*-like flowers and inflorescences, although differing markedly from *Lamarckiana* in habit and foliage.

I am greatly indebted to the Harvard botanic garden for the facilities placed at my disposal for this work.

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